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ORIGINAL RESEARCH

# Demographic monitoring of the invasive ladder snake on Formentera (Balearic Islands, Spain)

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## Abstract

The ladder snake *Zamenis scalaris* was first reported in 2006 in Formentera (Balearic Islands, Spain), until then a snake-free Mediterranean island. Since 2016, intense control campaigns have been carried out and, for the first time, snake captures over 2017–2020 have been used to analyze the sex ratio, age, fat percentage, population density, and seasonality of this invasive population. The male-biased sex ratio found in the present work could be the result of capture biases caused by different detection probabilities between sexes. A reduction of snake body length over time was observed, which could indicate a depletion of the larger snakes due to intense snake capture. The highest capture frequencies of both sexes were reported in May and June, coinciding with the mate searching period in the species native range and indicating that snakes increase their movements during this period. Size-specific survivorship curves indicated a drop in survivorship at medium sizes, which suggested a survival cost associated with reproduction, presumably due to increased mortality during the mating season. Population density decreased from 1.812 snakes/ha in 2017 to 0.669 snakes/ha in 2020. Evidence obtained in the present work has allowed to evaluate the main ecological aspects of *Z. scalaris* and the current state of the population of this invasive snake on the island of Formentera. Results showed that the population is well established in Formentera, but prolonged control campaigns have caused its decline. This study becomes a starting point to improve the management and control programs of invasive snake populations in the Balearic Islands. Long-term control as well as the improvement of the detection and capture of adult females are strongly recommended to attempt the eradication of *Z. scalaris* in Formentera.

## Introduction

Demographic analyses of wild populations involve assessing basic ecological parameters (Brown & Weatherhead, 1999; Jordan & Rodda, 1994; Montes, Feriche, et al., 2021; Park, 2004; Pleguezuelos et al., 2007) that are essential to understand the biology, trophic ecology, and reproductive traits of a species (Aldridge & Brown, 1995; Caughley, 1994; Ford & Seigel, 1989; Gibbons, 1972; Godley, 1980; Rose et al., 2013). Snakes' nocturnality, broad movements, low recapture rates, crypsis, and periods of inactivity (Durso & Seigel, 2015; Steen, 2010; Ward et al., 2017) may have prevented the study of their demography in the past. However, in recent years, the number of studies assessing snake populations introduced out of their native range has substantially grown (e.g., Cabrera-Pérez et al., 2012; Capinha et al., 2017; Christy et al., 2010; Guzy et al., 2023; Montes et al., 2020). Demographic studies are essential to determine the effect of environmental variables on life history (Blouin-Demers et al., 2002; Gregory & Larsen, 1996) and to manage invasive species (Park, 2004). These studies are crucial to analyze the establishment process of introduced populations out of their native range (Rose et al., 2013; Willson et al., 2011), understand the population dynamics (Jordan & Rodda, 1994), and define the life-history traits (Mathies et al., 2010; Moore et al., 2005; Pleguezuelos et al., 2007; Whittier & Limpus, 1996) of alien snake species.

Herpetological invasions are generally a direct consequence of international trade, as these animals are accidentally transported with cargo goods for human consumption or use, one of the main pathways being the transportation of live plants for ornamental purposes (Kraus, 2009). Snake introductions out of their native range have led to over 100 established populations worldwide (Capinha et al., 2017). Invasive snakes are one of the main drivers of species extinction worldwide (Rodda et al., 1997; Rodda & Fritts, 1992) and are extremely damaging in insular ecosystems (Fritts & Rodda, 1998) given the lack of pathogens, parasites, and predators in the new territory, which is commonly termed as the enemy release hypothesis (Montes et al., 2020; Roy et al., 2011). These impacts are exemplified by the brown tree snake *Boiga irregularis* (Bechstein, 1802) in Guam, which has caused the loss of native species (Rodda et al., 1997; Rodda & Fritts, 1992; Rodda & Savidge, 2007; Wiles et al., 2003). The recently introduced horseshoe whip snake *Hemorrhois hippocrepis* (Linnaeus, 1758) in Eivissa (Balearic Islands, Spain) (Montes, Pleguezuelos, et al., 2021) and the California kingsnake *Lampropeltis californiae* (Blainville, 1835) in Gran Canaria (Canary Islands, Spain; Cabrera-Pérez et al., 2012; Monzón-Argüello et al., 2015; Piquet & López-Darias, 2021) are also known to prey upon native reptiles and pose a serious threat to their populations. In addition, snake introductions can also lead to ecosystem degradation (Fritts & Rodda, 1998) and have socioeconomic impacts (Soto et al., 2022; Zhang et al., 2022).

The ladder snake *Zamenis scalaris* (Schinz, 1822) is a medium-sized colubrid that inhabits most of the Iberian Peninsula and southeastern France (Pleguezuelos & Honrubia, 2002). *Zamenis scalaris* was introduced on Menorca (Balearic Islands) in Roman times from the Iberian Peninsula (Vigne & Alcover, 1985), where it is widely distributed. More recently, this species has been introduced on the remaining islands of the archipelago, since it was reported for the first time on Eivissa in 2003, on Mallorca in 2004, and on Formentera in 2006 (Álvarez et al., 2010; Mateo et al., 2011; Pinya & Carretero, 2011), these two last islands being free of snakes until then (Silva-Rocha et al., 2015). The species was apparently introduced via nursery trade from the Iberian Peninsula, mainly related to olive trees (Álvarez et al., 2010). Although *Z. scalaris* mainly feeds on mammals and birds (Pleguezuelos et al., 2007; Vericad & Escarré, 1976), some authors suggest that some native species inhabiting Formentera, such as the endemic lizard *Podarcis pityusensis* (Boscá, 1883), could be under threat because of this recently introduced species (Pleguezuelos, 2019). However, potential threats to this native lizard and also to mammals and birds are highly understudied. Currently, all species of the family Colubridae inhabiting Formentera are considered legally invasive, given the inclusion in the Spanish Catalogue of Invasive Alien Species (Real Decreto 630/2013, 2013). For this reason, control and eradication campaigns have been carried out there since 2016 by the Department of Health and Control of Fauna of the Consortium for the Recovery of Fauna of the Balearic Islands (COFIB). As no assessment has been conducted so far on this invasive species, this study becomes essential to obtain information on the ecological aspects of *Z. scalaris* on the recently invaded island of Formentera.

The present study aimed to better understand the biology and ecology of the introduced snake *Z. scalaris* on a recently invaded island as well as evaluating the potential effects and results of the snake control campaigns carried out on the island of Formentera. The hypothesis of this work is that the analyses of biometric parameters, structure, and dynamics of the population would indicate the establishment of the colubrid *Z. scalaris* on the island of Formentera more than 10 years after it had first been reported. In addition, the hypothesis for snake population density in Formentera is that this parameter would decrease throughout the years of study because of the intense control and eradication campaigns carried out since 2016 by the COFIB. Thus, the specific aims of this study were (1) to describe the main biometric parameters, the structure, and the dynamics of the population over the 4 years of study, (2) to analyze the variations in size, age, fat percentage, and density of the population over time and (3) to assess the main activity period of the species in the newly invaded area.

## Materials and methods

### Study area, capture of individuals, and data collection

Snakes used for the present work were captured under the framework of control campaigns carried out by the COFIB and the local Government of the Balearic Islands. In these campaigns, a new snake live trap designed by the COFIB was used for the first time (MITECO, 2018; Picó et al., 2019; Fig. S1) following the protocol specified by Picó et al. (2019). In this trap, the entrance for snakes consisted of a one-way flap door, since it prevents escapes and allows multiple captures (Boyarski et al., 2008; Engeman et al., 2018).

Captured individuals were euthanized with pentobarbital (0.1 ml 100 $g^{-1}$) by the Department of Health and Control of Fauna of the COFIB. The snakes were preserved at −20°C until these specimens were given to the University of the Balearic Islands for further analyses. As the individuals were euthanized by qualified staff from the COFIB, no ethical approval was needed for the realization of the present work at the University of the Balearic Islands. After the analyses, all animal remains were incinerated by COFIB in accordance with national regulations on animal by-products nonintended for human consumption (SANDACH).

Fieldwork was carried out from March to November of the years 2017, 2018, 2019, and 2020 at La Mola, a plateau located in the southeast of the island of Formentera (Ferrer-Abárzuza, 2015; Fig. 1). Mean temperatures in La Mola are approximately 10°C in winter and 25°C in summer (AEMET, 2011). For each snake that was captured, GPS location and capture date were collected. Sex was identified by inserting a sexing probe into the vent and by examining gonads during necropsy. Snout-vent length (SVL) was measured with a flexometer (to the nearest 1 mm) and body mass was weighed with an electronic scale (Adam Equipment, Milton Keynes, UK). Fat bodies of the snakes were extracted during necropsies and the fat mass was weighed with an electronic scale (Cobos Precision, L'Hospitalet de Llobregat, Barcelona). The finding of oviductal eggs in females during necropsy was considered. Juvenile and adult life stages were established according to the sexual maturity of specimens, following Pleguezuelos and Feriche (2006) (adult males ≥ 450 mm SVL, adult females ≥ 660 mm SVL).

## Age determination

To determine snake age, the ectopterygoid bone was extracted and analyzed through skeletochronology techniques (Castanet, 1994). Ectopterygoid bones were cleaned with sodium hypochlorite 10% before their observation to remove the soft tissues (Biasatti, 2004). Bones were kept in water to increase bone transparency and contrast between skeletal growth marks (SGM; Castanet et al., 1993). After this procedure, SGM were read with a binocular microscope LEICA DM 2500P 40x (LEICA, Wetzlar, Germany) under transmitted light (Fornasiero et al., 2016). SGM counting was performed by two researchers and parallel readings were compared. In case of disagreement, growth marks were counted again and the sample was discarded if the discrepancy persisted.

## Statistical analyzes

Statistical analyses were performed using R v.1.1.453 (R Core Team, 2022). The protocol proposed by Zuur et al. (2010) was carried out to explore the data. Statistical significance was considered at $P < 0.05$. Chi-squared tests of goodness of fit were used to assess the sex ratio and adult–juvenile ratio of captured individuals. Fat percentage (total wet fat mass/total wet body mass * 100; %) was used as a measure of body condition after confirming that this parameter was not biased with respect to body length through regression analyses, according to previous works (Falk et al., 2017; Peig & Green, 2009; Schamber et al., 2009; Schulte-Hostedde et al., 2005; Weatherhead & Brown, 1996). Captured individuals were classified into 10-cm size classes and size–frequency distributions for each sex were plotted. Residual plots were used to check the normality and heterogeneity of the variance in the residuals and the Durbin-Watson test was used to check the autocorrelation of the residuals. An analysis of covariance (ANCOVA) was performed to examine the influence of sex, year of study, and the interaction of these two factors on the continuous variable SVL, including age as a covariate. A two-way analysis of variance (two-way ANOVA) was carried out to examine the influence of sex, year of study, and the interaction of these two factors on the continuous variable fat percentage. *Post hoc* pairwise comparisons with Holm's correction for multiple tests were performed for both ANCOVA and ANOVA. For the analysis of the seasonality of population activity period, the frequency of males and females that were captured during each sampling month was evaluated for all study years. Fat percentage (%) of adult females in each month of the year was calculated.

For the study of size-specific survivorship ($l_x$), individuals were classified into 10-cm size classes. Size-specific survivorship ($l_x$) was analyzed for both sexes and survivorship curves

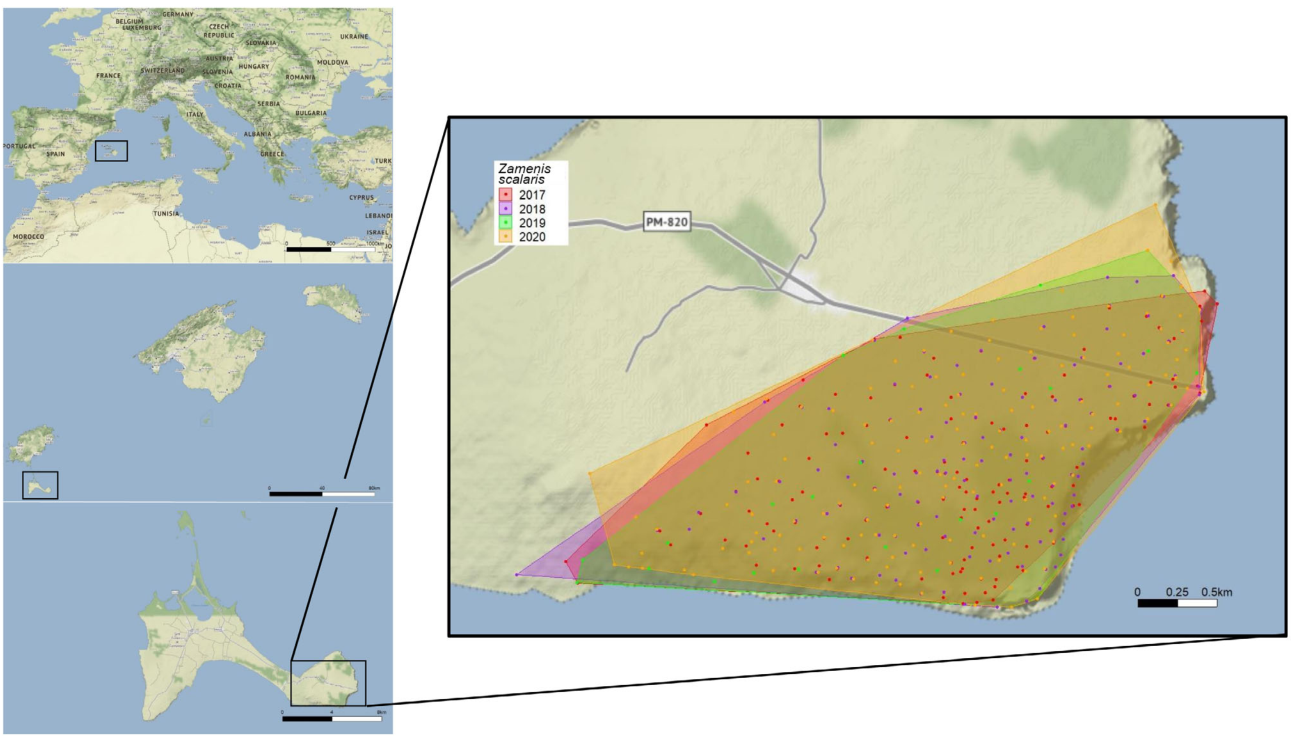


**Figure 1** Distribution area of the snakes captured on the island Formentera for the period 2017–2020 obtained using the minimum convex polygon method. GPS locations of the traps in which at least one snake was captured are also indicated.

were plotted for males and females each year of the study. Size-specific survivorship ($l_x$) is the proportion of survivors when cohort x begins (Riedle, 2014).

Leslie depletion method (package 'FSA', function 'depletion', method 'Leslie'; Ogle et al., 2023) was performed to estimate the initial population size of snakes through the regression of weekly catch per unit effort (CPUE) and cumulative catch of snakes (Leslie & Davis, 1939; Ricker, 1975; Rose et al., 2013). The unit effort referred to trap-nights which were calculated using the number of traps that lasted active in the field per night. The estimated population size, the 95% confidence interval (CI), relative standard error (RSE), $R^2$ of the regression, and regression significance were assessed for each year of study (2017–2020). The area of distribution of the captured snakes was obtained by conducting the minimum convex polygon method using a statistical package (package "adehabitatHR"; Calenge, 2006). To obtain the estimated density of snakes (snakes/ha), the estimated population size was divided by the obtained area of distribution.

# Results

## Number of captures and sex ratio

Total number of *Z. scalaris* individuals captured was 964 in 2017, 513 in 2018, 419 in 2019, and 508 in 2020. Sex ratio was significantly biased in favor of males in 2017 (1:0.88, $X^2 = 4.51$, d.f. = 1, $P < 0.05$), 2019 (1:0.76, $X^2 = 7.23$, d.f. = 1, $P < 0.01$), and 2020 (1:0.82, $X^2 = 5.16$, d.f. = 1, $P < 0.05$), whereas it did not statistically differ from 1:1 in 2018 (1:0.88, $X^2 = 2.14$, d.f. = 1, $P > 0.05$). Adult–juvenile ratio was biased in favor of adults throughout the study period (1:0.40, $X^2 = 185.23$, d.f. = 1, $P < 0.0001$ in 2017; 1:0.55, $X^2 = 44.12$, d.f. = 1, $P < 0.0001$ in 2018; 1:0.53, $X^2 = 34.56$, d.f. = 1, $P < 0.0001$ in 2019; 1:0.66, $X^2 = 21.73$, d.f. = 1, $P < 0.0001$ in 2020).

## Snout-vent length, age, fat percentage, and activity season

Females showed larger body lengths than males and a significant decrease in SVL was observed across the years (Fig. 2, Table S1). Snakes' age ranged from 1 to 20 years in males and from 1 to 19 years in females (Table 1). A slight decrease in age was observed in males and an increase was detected in females over the years of study (Table 1). Snake SVL varied statistically between sexes (ANCOVA, $F_{1,1072} = 5.02$, $P < 0.005$) and across years (ANCOVA, $F_{1,1072} = 12.34$, $P < 0.0001$), except for 2018–2019 ($P = 0.39$) and 2019–2020 ($P = 0.08$; Fig. 2, Table S1). No interaction between sex and year was detected (ANCOVA, $F_{2,1072} = 1.69$, $P = 0.19$) and no significant influence of age on SVL was observed (ANCOVA, $F_{1,1072} = 0.66$, $P = 0.42$). Females showed higher fat percentages than males and fat percentages increased over the years of study (Fig. 2, Table S1). Fat percentage differed statistically between sexes (ANOVA, $F_{1,748} = 6.85$, $P < 0.01$) and across years (ANOVA, $F_{1,748} = 23.58$, d.f. = 1, $P < 0.0001$), except for 2019–2020 ($P = 0.30$). No interaction between sex and year was detected (ANOVA, $F_{2,748} = 0.34$, $P = 0.56$).

Frequency of captures of both sexes increased gradually from March until May (2018) or June (2017, 2019, and 2020; Fig. 3). A progressive decrease was observed from July until the end of the campaign in November. However, a slight increase in captures was observed in August 2017, September and October 2018 and 2019, thus evidencing a second peak of captures. Only four captured females carried oviductal eggs and all of them were captured during the second half of June. Adult female fat percentage was considerably high year-round (Table S2).

## Survivorship

The size-specific survivorship ($l_x$) of small and large snakes remained stable across the years of study while the steepest decline affected medium sizes (Figs. 4 and 5). There seemed

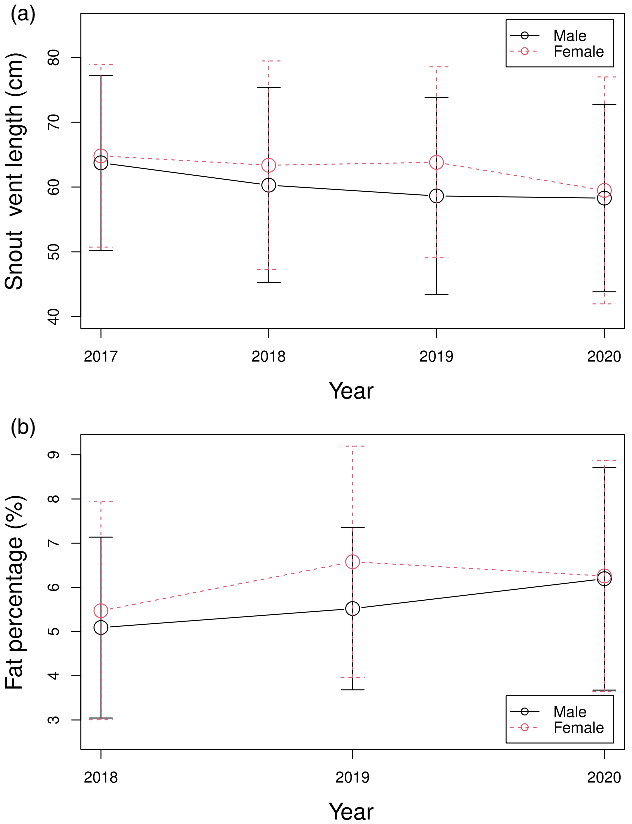


**Figure 2** Variation of (a) snout-vent length (SVL) and (b) fat percentage (%) over 2017–2020. Mean values are represented by empty circles and standard deviations (SD) by error bars. The sample sizes used in (a) were $n = 511$ in 2017, $n = 270$ in 2018, $n = 211$ in 2019, and $n = 278$ in 2020 for males and $n = 450$ in 2017, $n = 238$ in 2018, $n = 161$ in 2019 and $n = 227$ in 2020 for females. The sample sizes used in (b) were $n = 227$ in 2018, $n = 74$ in 2019, and $n = 90$ in 2020 for males and $n = 198$ in 2018, $n = 52$ in 2019, and $n = 111$ in 2020 for females.

**Table 1** Mean ± standard deviation (SD), range (minimum value–maximum value), and sample sizes of age (in years) of male and female *Zamenis scalaris* captured in 2017–2019

| | 2017 | 2018 | 2019 |
|---|---|---|---|
| Males | 8.47 ± 3.18 (1–19) *n* = 315 | 8.07 ± 4.06 (1–20) *n* = 204 | 7.9 ± 3.99 (1–18) *n* = 70 |
| Females | 8.55 ± 3.39 (1–19) *n* = 255 | 8.67 ± 4.01 (1–19) *n* = 181 | 8.91 ± 4.05 (1–16) *n* = 47 |

to be a sex bias in medium sizes, given the drop in survivorship in females that was observed at slightly larger body lengths than males (Figs. 4 and 5).

## Population density

Leslie depletion method estimated population size (95% CI; RSE) as 1297 (951–1642; 13.6%) in 2017, 614 (487–741; 10.5%) in 2018, 759 (130–1387; 42.2%) in 2019 and 549 (471–627; 7.2%) in 2020. Estimated density of snakes was 1.812 snakes/ha in 2017, 0.801 snakes/ha in 2018, 1.037 snakes/ha in 2019, and 0.669 snakes/ha in 2020, so, results showed a clear downward trend in the density of snakes. CPUE was strongly and significantly related to cumulative catches across all years ($R^2 > 0.3$ and $P < 0.0001$ in all cases), except 2019 ($R^2$: 0.07, $P = 0.07$; Fig. S2). This and the high SE found in 2019 suggested snake population estimates for that year were unreliable.

# Discussion

Results obtained on *Z. scalaris* demographic parameters evidence a successful establishment of the ladder snake on the island of Formentera. Based on previous evidence on snake invasions (Kraus, 2009; Piquet & López-Darias, 2021; Shwiff et al., 2010), this insular ecosystem and its native fauna could be strongly affected by ecological and socioeconomic impacts. Although management plans have proven to be effective for capturing snakes, results show that the recruitment capacity of juveniles has not declined. This fact suggests that trapping

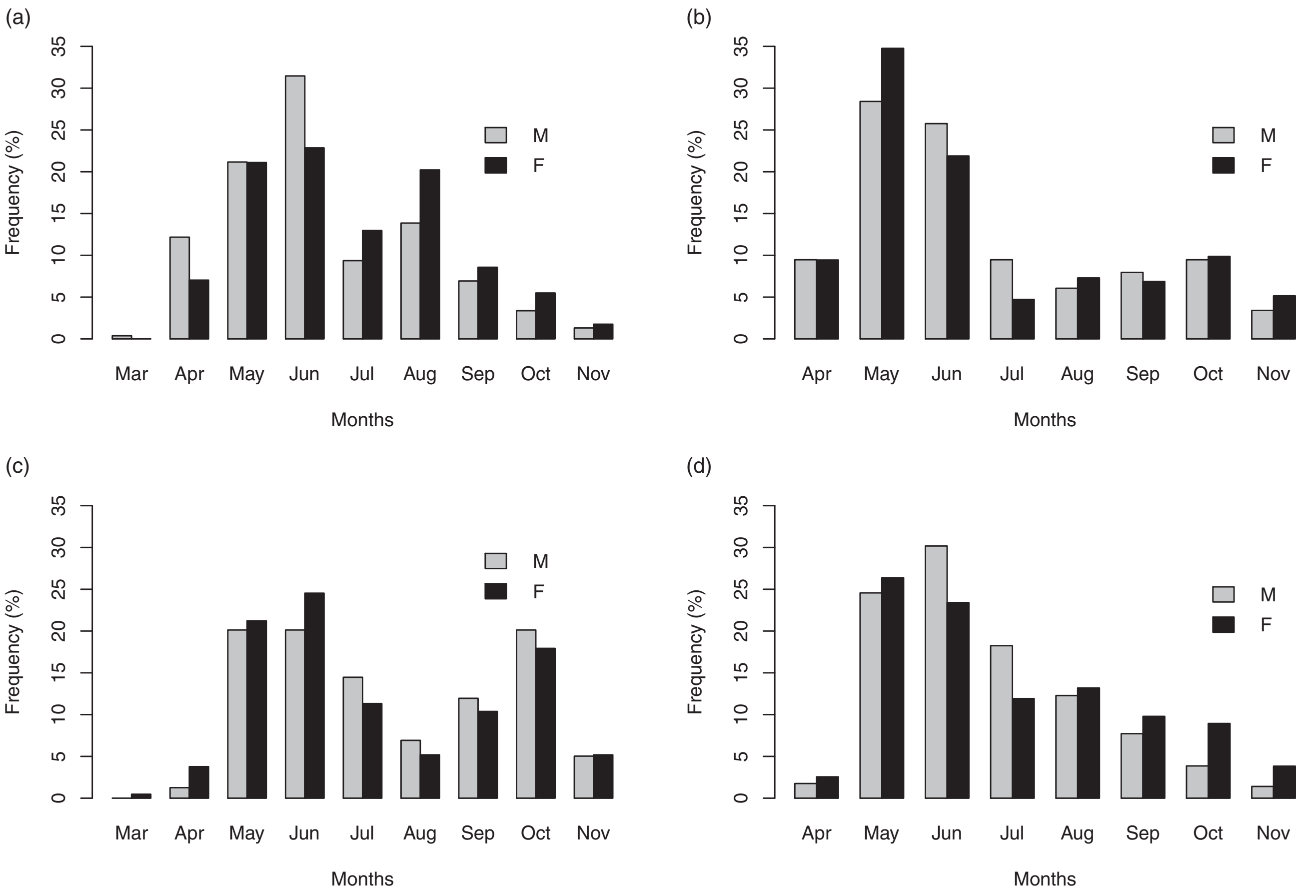


**Figure 3** Relative frequency of capture of adult male and adult female *Zamenis scalaris* during each sampling month (March–November) of the years 2017–2020 (a-d). The sample sizes used were *n* = 505 in 2017, *n* = 220 in 2018, *n* = 168 in 2019, and *n* = 229 in 2020 for males and *n* = 207 in 2017, *n* = 101 in 2018, *n* = 74 in 2019, and *n* = 83 in 2020 for females.

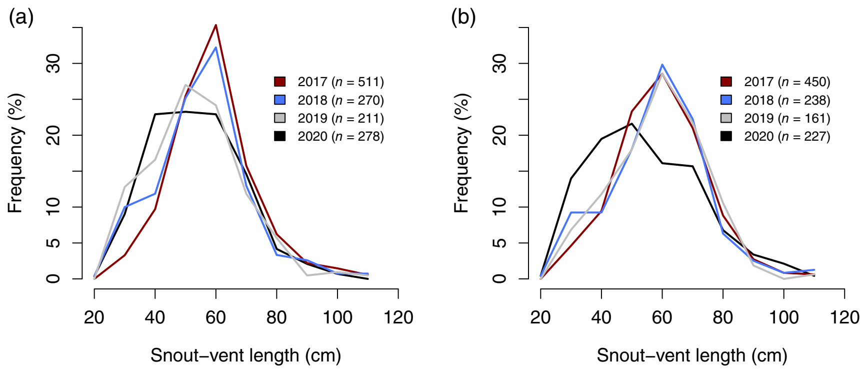


**Figure 4** Size–frequency distribution of captured (a) male and (b) female *Zamenis scalaris* on Formentera during the years 2017–2020.

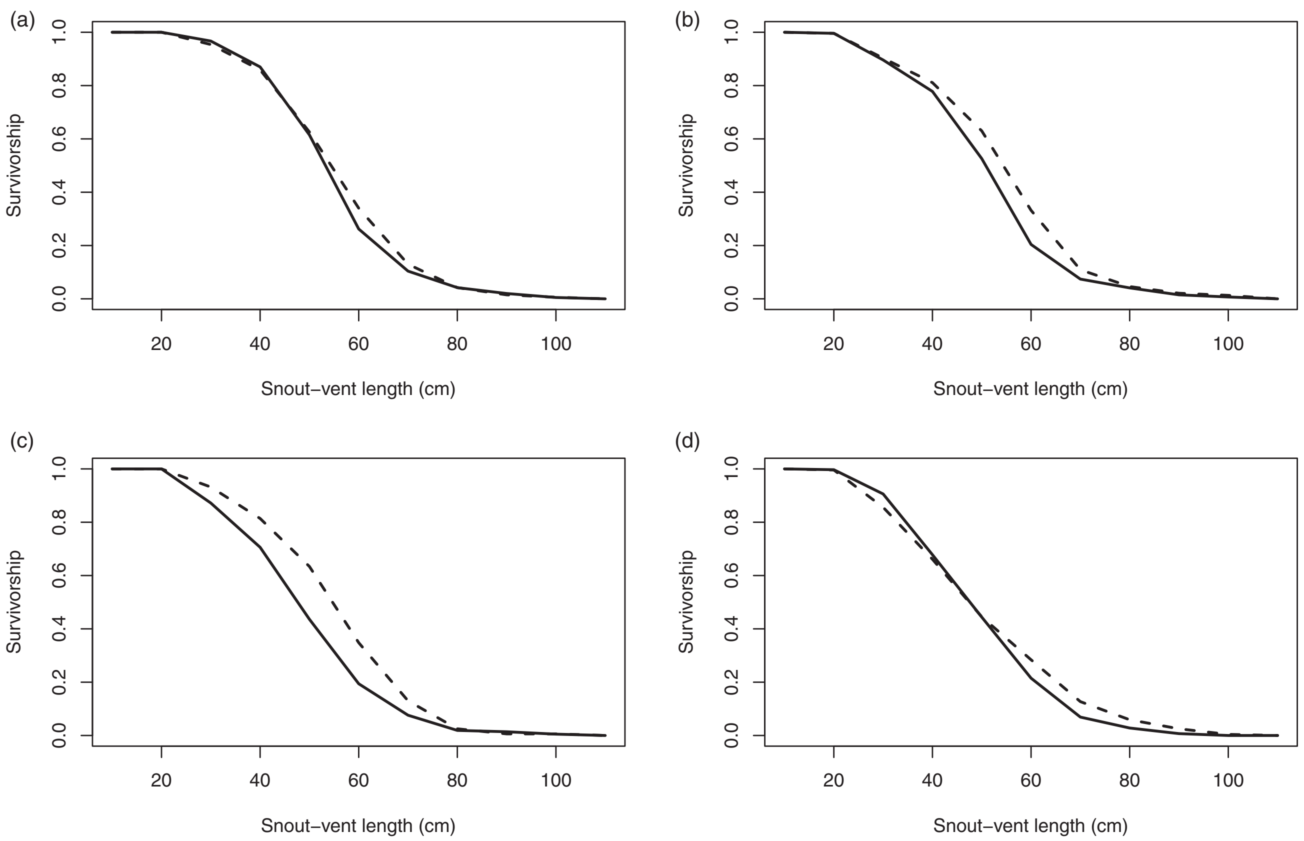


**Figure 5** Size-specific survivorship ($l_x$) of males (solid lines) and females (dashed lines) of *Zamenis scalaris* on Formentera during the years (a) 2017, (b) 2018, (c) 2019, and (d) 2020. The sample sizes used were $n$ = 511 in 2017, $n$ = 270 in 2018, $n$ = 211 in 2019, and $n$ = 278 in 2020 for males and $n$ = 450 in 2017, $n$ = 238 in 2018, $n$ = 161 in 2019, and $n$ = 227 in 2020 for females.

efforts should be continued or even intensified over time to increase management effectiveness. Furthermore, locating the mating areas of the population and intensifying the captured pressure on adult females are strongly recommended.

Sex ratio was significantly biased in favor of males. Sexual size dimorphism in favor of females and a significant decrease in SVL were observed across the years of study, as well as an increase in fat percentage. Females showed higher fat percentages than males. Sex ratios are believed to be related to sex differences in behavior instead of deviations from balanced sex ratios in snake populations (Iverson, 1990; Shine et al., 2007). This is mainly due to seasonal reproductive processes that influence movement patterns and vulnerability to predation (Bonnet et al., 1999). Whereas females are more cryptic (Shine et al., 2007), males move more frequently and over longer distances during the mating season (Aldridge &

Brown, 1995; Bonnet et al., 1999; Savidge, 1991; Shine et al., 2007). Therefore, sex ratio differences should be considered capture biases as they are based on activity patterns, often related to seasonality and reproduction (Chaitae, 2011). In addition, the sexual size dimorphism observed could also be caused by a capture bias, as body size could affect detectability differently in each sex (Christy et al., 2010; Guzy et al., 2023). This capture bias could have many implications for the invasion process as certain sizes could escape detection and capture, leading to population expansion. Besides, environmental selection pressures such as resource limitation are believed to affect body size and generate variation in sexual size dimorphism (Brown et al., 2017; Winne et al., 2010). This fact should also be considered in the present work since different resource availability could be found between native and receiving areas.

Frequency of captures showed two peaks, the first being in spring (May or June) and the second in late summer or autumn (August–October). Two periods of higher activity during spring and autumn are generally observed in the native area of the ladder snake (Feriche, 1998). In the present work, the highest frequencies of both males and females were observed in May and June, which coincides with those of the native area (Feriche, 1998; Pleguezuelos & Brito, 2008). According to some authors, the second peak of captures observed in autumn is mostly caused by females (Feriche, 1998) or neonates, as hatching occurs during late September and early October (Blázquez, 1993; Pleguezuelos & Feriche, 2006). Frequency of females was higher than that of males in the second peak of captures observed in 2017 but not in 2018 and 2019. However, between none and two neonates were found each year, considering the sizes of neonates proposed by Pleguezuelos and Feriche (2006). Regarding energy stores, the high-fat percentage obtained year-round suggested no relationship between the reproductive cycle and fat storage of adult females, as reported in the native area (Pleguezuelos & Feriche, 2006). This might be explained by the ladder snake feeding even during the vitellogenesis period (Pleguezuelos & Feriche, 2006), except during the final stage of oviductal eggs (Blázquez, 1994; Pleguezuelos & Feriche, 2006). These data are of great relevance to improve the effectiveness of the management actions, as the high frequency of captures reported during May and June would indicate a suitable period to increase the captured pressure. All the obtained results evidence the need to detect and remove more adult females. Therefore, additional management actions such as the analysis of the geographic data on snake capture combined with data on seasonality could be of great relevance to locate the breeding areas of the population and intensify the captured pressure there during the mating period.

Size-specific survivorship ($l_x$) indicated a drop in survivorship at medium sizes, thus appearing to describe a survival cost associated with reproduction (Brown & Weatherhead, 1999; Madsen & Shine, 1993). Reduction of survivorship in sexually mature males has often been associated with increased movements during the mating season (Aldridge & Brown, 1995; Bonnet et al., 1999; Brown & Weatherhead, 1999; Shine et al., 2007) while in females, lower survivorship is often related to higher mortality during the egg-laying migration (Bonnet et al., 1999; Madsen & Shine, 1993). Nevertheless, the downward trend observed in body length could be caused by the intense control campaigns carried out, as the capture effort exerted could have acted as a selection pressure. Overharvesting is known to cause the depletion of larger size classes of a population and a reduction in the age and size at maturity, as described for fisheries (Allan et al., 2005; Fenberg & Roy, 2008; Heino & Godø, 2002; Sardá, 1998; Trippel, 1995). Frequencies of large snakes remained similar across the years and frequencies of small snakes increased, especially in 2020, which could lead to higher recruitment of hatchlings and a high reproduction rate of large snakes. A growth in population abundance due to an increase in juveniles and high fecundity of adults can be produced in response to a massive removal of individuals in a population, something which is known as overcompensation (e.g., Guzy et al., 2023). Nevertheless, further research on this observation for longer periods of time would be needed to test this hypothesis. In addition, control and eradication measures should be continued and even intensified to try to deplete the larger size classes, especially females.

A downward trend in the population size was observed over the years of study, which indicates that the removal efforts reduced the population size. Snake density correspondingly decreased from 1.812 snakes/ha in 2017 to 0.669 snakes/ha in 2020, probably because of the successive and prolonged control programs carried out. Given that control effort success is strongly affected by the ability to monitor shifts in population abundance (Guzy et al., 2023), obtaining a robust and feasible population estimation becomes a crucial tool to manage this invasive population. The observed downward trend in the population size encourages the continuation of the capture efforts that are currently carried out since they are apparently giving successful results. It should be noted that determining snake abundance and density is extremely challenging due to their cryptic habits (Steen, 2010; Ward et al., 2017). Therefore, models used to infer population size and density often produce unreliable outputs, such as when there is no consideration for detectability biases (Amburgey et al., 2021; Ward et al., 2017), given that if the detectability is low, then the utility of the model is limited in generating reliable abundance estimates (Steen, 2010). Depletion methods also become inaccurate when the proportion of individuals removed is small, which can lead to an overestimation in the estimated population size (Ogle, 2018). In addition, capture biases, the fact that the population may not have been closed and variable catchability over time could also be potential sources of error when performing Leslie depletion models that should be taken into account. For these reasons, the use of alternative methods such as removal models (Rodríguez de Rivera & McCrea, 2021), capture-mark-recapture techniques (Godley, 1980; Plummer, 1985; Riedle, 2014), presence–absence surveys (Pollock, 2006), or a combination of various population estimation methods (Rose et al., 2013) should be considered to evaluate potential biases in the results obtained.

Actions aimed at improving the management plans should prioritize prevention measures and pathways of introductions

(Hulme, 2009; Kraus, 2009), a fact that has been recently addressed by the local administration of the Balearic Islands (Decret llei 1/2023, 2023). Developing early detection and rapid response protocols (Simberloff et al., 2013) and sustained campaigns until demographic collapse is observed (Guzy et al., 2023) are also essential management actions. However, the results obtained in the present work evidence the need to capture mature females. For this reason, a comprehensive analysis of the geographic data on snake captures in order to locate the mating areas of the population should be addressed. Capture pressure could be intensified geographically and temporally, by concentrating capture effort in areas frequented by adult females and during the period of activity of the snakes which coincides with the mating period of the species in its native area (May and June). By combining geographic and temporal data, trapping efforts could be directed at adult females who are the main target individuals in a management campaign. Furthermore, trophic ecology studies and the identification of oviposition sites would also increase management effectiveness and avoid the potential recovery of this invasive population. Although further research is needed, this study becomes a starting point not only to improve the management of *Z. scalaris* population in Formentera but also to extrapolate it to other invasive snakes worldwide.

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## References

AEMET. (2011). *Atlas Climático Ibérico–Iberian Climate Atlas*. AEMET, Agencia Estatal de Meteorología, Ministerio de Medio Ambiente y Medio Rural y Marino. IM, Instituto de Meteorologia de Portugal https://doi.org/10.31978/784-11-002-5

Aldridge, R. D., & Brown, W. S. (1995). Male reproductive cycle, age at maturity, and cost of reproduction in the timber rattlesnake (*Crotalus horridus*). *Journal of Herpetology*, **29**(3), 399–407. https://doi.org/10.2307/1564990

Allan, J. D., Abell, R., Hogan, Z. E. B., Revenga, C., Taylor, B. W., Welcomme, R. L., & Winemiller, K. (2005). Overfishing of inland waters. *Bioscience*, **55**(12), 1041–1051. https://doi.org/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2

Álvarez, C., Mateo, J. A., Oliver, J., & Mayol, J. (2010). Los ofidios ibéricos de introducción reciente en las Islas Baleares. *Boletín de la Asociación Herpetológica Española*, **21**, 126–131.

Amburgey, S. M., Yackel Adams, A. A., Gardner, B., Hostetter, N. J., Siers, S. R., McClintock, B. T., & Converse, S. J. (2021). Evaluation of camera trap-based abundance estimators for unmarked populations. *Ecological Applications*, **31**(7), e02410. https://doi.org/10.1002/eap.2410

Biasatti, D. M. (2004). Stable carbon isotopic profiles of sea turtle humeri: Implications for ecology and physiology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **206**(3–4), 203–216. https://doi.org/10.1016/j.palaeo.2004.01.004

Blázquez, M. C. (1993). *Ecología de dos especies de colúbridos Malpolon monspessulanus y Elaphe scalaris en Doñana (Huelva)*. Doctoral thesis. Universidad de Sevilla, Sevilla.

Blázquez, M. C. (1994). Notes on the reproduction of *Elaphe scalaris* (Schinz, 1822) in Southern Spain. *Herpetological Journal*, **4**(3), 109–111.

Blouin-Demers, G., Prior, K. A., & Weatherhead, P. J. (2002). Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. *Journal of Zoology*, **256**(1), 1–10. https://doi.org/10.1017/S0952836902000018

Bonnet, X., Naulleau, G., & Shine, R. (1999). The dangers of leaving home: Dispersal and mortality in snakes. *Biological Conservation*, **89**(1), 39–50. https://doi.org/10.1016/S0006-3207(98)00140-2

Boyarski, V. L., Savidge, J. A., & Rodda, G. H. (2008). Brown treesnake (*Boiga irregularis*) trappability: Attributes of the snake, environment and trap. *Applied Herpetology*, **5**(1), 47–61. https://doi.org/10.1163/157075408783489239

Brown, G. P., Madsen, T. R., & Shine, R. (2017). Resource availability and sexual size dimorphism: Differential effects of prey abundance on the growth rates of tropical snakes. *Functional Ecology*, **31**(8), 1592–1599. https://doi.org/10.1111/1365-2435.12877

Brown, G. P., & Weatherhead, P. J. (1999). Demography and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology*, **77**(9), 1358–1366. https://doi.org/10.1139/z99-112

Cabrera-Pérez, M. Á., Gallo-Barneto, R., Esteve, I., Patiño-Martínez, C., & López-Jurado, L. F. (2012). The management and control of the California kingsnake in gran canaria (Canary Islands): Project life+ lampropeltis. *Aliens: The Invasive Species Bulletin*, **32**, 20–28.

Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Capinha, C., Seebens, H., Cassey, P., García-Díaz, P., Lenzner, B., Mang, T., Moser, D., Pyšek, P., Rödder, D., Scalera, R., Winter, M., Dullinger, S., & Essl, F. (2017). Diversity, biogeography and the global flows of alien amphibians and reptiles. *Diversity and Distributions*, **23**(11), 1313–1322. https://doi.org/10.1111/ddi.12617

Castanet, J. (1994). Age estimation and longevity in reptiles. *Gerontology*, **40**(2–4), 174–192. https://doi.org/10.1159/000213586

Castanet, J., Francillon-Vieillot, H., Meunier, F. J., & De Ricqles, A. (1993). Bone and individual aging. In B. K. Hall (Ed.), *Bone – A treatise* (pp. 245–283). CRC Press.

Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology*, **63**(2), 215–244. https://doi.org/10.2307/5542

Chaitae, A. (2011). *Demography of the Monocled cobra (Naja kaouthia) in the central region of Thailand. Electronic theses and dissertations. University of Louisville* https://doi.org/10.18297/etd/228

Christy, M. T., Yackel Adams, A. A., Rodda, G. H., Savidge, J. A., & Tyrrell, C. L. (2010). Modelling detection probabilities to evaluate management and control tools for an invasive species. *Journal of Applied Ecology*, **47**(1), 106–113. https://doi.org/10.1111/j.1365-2664.2009.01753.x

Durso, A. M., & Seigel, R. A. (2015). A snake in the hand is worth 10,000 in the bush. *Journal of Herpetology*, **49**(4), 503–506. https://doi.org/10.1670/15-49-04.1

Engeman, R. M., Shiels, A. B., & Clark, C. S. (2018). Objectives and integrated approaches for the control of brown tree snakes: An updated overview. *Journal of Environmental Management*, **219**, 115–124. https://doi.org/10.1016/j.jenvman.2018.04.092

Falk, B. G., Snowm, R. W., & Reed, R. N. (2017). A validation of 11 body-condition indices in a giant snake species that exhibits positive allometry. *PLoS One*, **12**(7), e0180791. https://doi.org/10.1371/journal.pone.0180791

Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology*, **17**(1), 209–220. https://doi.org/10.1111/j.1365-294X.2007.03522.x

Feriche, M. (1998). *Ecología de la reproducción en colúbridos del sureste de la Península Ibérica*. Doctoral Thesis. Universidad de Granada, Granada.

Ferrer-Abárzuza, A. (2015). *Una infraestructura ramadera andalusí? Proposta d'adscripció cronològica dels aljubs de la Mola (Formentera, Illes Balears)*. Irrigation, Society and LandscapeTribute to Tom F. Glick, 301–318 https://doi.org/10.4995/ISL2014.2014.165

Ford, N. B., & Seigel, R. A. (1989). Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica*, **45**(1), 75–83.

Fornasiero, S., Bonnet, X., Dendi, F., & Zuffi, M. (2016). Growth, longevity and age at maturity in the European whip snakes, *Hierophis viridiflavus* and *H. carbonarius*. *Acta Herpetologica*, **11**(2), 135–149. https://doi.org/10.13128/Acta_Herpetol-18695

Fritts, T. H., & Rodda, G. H. (1998). The role of introduced species in the degradation of Island ecosystems: A case history of Guam. *Annual Review of Ecology and Systematics*, **29**(1), 113–140. https://doi.org/10.1146/annurev.ecolsys.29.1.113

Gibbons, J. W. (1972). Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia*, **1972**(2), 222–226. https://doi.org/10.2307/1442480

Godley, J. S. (1980). Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. *Ecological Monographs*, **50**(4), 411–436. https://doi.org/10.2307/1942651

Gregory, P. T., & Larsen, K. W. (1996). Are there any meaningful correlates of geographic life-history variation in the garter snake, *Thamnophis sirtalis*? *Copeia*, **1996**(1), 183–189. https://doi.org/10.2307/1446954

Guzy, J. C., Falk, B. G., Smith, B. J., Willson, J. D., Reed, R. N., Aumen, N. G., Avery, M. L., Bartoszek, I. A., Campbell, E., Cherkiss, M. S., Claunch, N. M., Currylow, A. F., Dean, T., Dixon, J., Engeman, R., Funck, S., Gibble, R., Hengstebeck, K. C., Humphrey, J. S., … Hart, K. M. (2023). Burmese pythons in Florida: A synthesis of biology, impacts, and management tools. *NeoBiota*, **80**, 1–119. https://doi.org/10.3897/neobiota.80.90439

Heino, M., & Godø, O. R. (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, **70**(2), 639–656.

Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**(1), 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Iverson, J. B. (1990). Sex ratios in snakes: A cautionary note. *Copeia*, **1990**(2), 571–573. https://doi.org/10.2307/1446364

Jordan, M. A., & Rodda, G. H. (1994). Identification of sex in *Boiga irregularis*: Implications for understanding population dynamics in Guam. *Journal of Herpetology*, **28**(3), 381–384. https://doi.org/10.2307/1564541

Kraus, F. (2009). *Alien reptiles and amphibians: A scientific compendium and analysis*. Springer.

Leslie, P. H., & Davis, D. H. S. (1939). An attempt to determine the absolute number of rats on a given area. *The Journal of Animal Ecology*, **8**(1), 94–113.

Madsen, T., & Shine, R. (1993). Costs of reproduction in a population of European adders. *Oecologia*, **94**(4), 488–495. https://doi.org/10.1007/BF00566963

Mateo, J. A., Ayres, C., & López-Jurado, L. F. (2011). Los anfibios y reptiles naturalizados en España: Historia y evolución de una problemática creciente. Historia y evolución de una problemática creciente. *Boletín de la Asociación Herpetológica Española*, **22**, 1–42.

Mathies, T., Cruz, J. A., Lance, V. A., & Savidge, J. A. (2010). Reproductive biology of male brown treesnakes (*Boiga irregularis*) on Guam. *Journal of Herpetology*, **44**(2), 209–221. https://doi.org/10.1670/06-069.1

MITECO. (2018). *Estrategia de gestión, control y posible erradicación de ofidios invasores en islas*. Ministerio para la Transición Ecológica. Gobierno de España.

Montes, E., Feriche, M., Alaminos, E., & Pleguezuelos, J. M. (2020). The horseshoe whip snake (*Hemorrhois hippocrepis*) on Ibiza: Predator release in an invasive population. *Amphibia-Reptilia*, **42**(2), 249–254. https://doi.org/10.1163/15685381-bja10039

Montes, E., Feriche, M., Ruiz-Sueiro, L., Alaminos, E., & Pleguezuelos, J. M. (2021). Reproduction ecology of the recently invasive snake *Hemorrhois hippocrepis* on the Island of Ibiza. *Current Zoology*, **66**, 363–371. https://doi.org/10.1093/CZ/ZOZ059

Montes, E., Pleguezuelos, J. M., & Kraus, F. (2021). Rapid endangerment of the lizard *Podarcis pityusensis* by an invasive snake demands an immediate conservation response. *Amphibian & Reptile Conservation*, **15**(2), 238–243.

Monzón-Argüello, C., Patiño-Martínez, C., Christiansen, F., Gallo-Barneto, R., Cabrera-Pérez, M. Á., Peña-Estévez, M. Á., López-Jurado, M. F., & Lee, P. L. (2015). Snakes on an Island: Independent introductions have different potentials for invasion. *Conservation Genetics*, **16**(5), 1225–1241. https://doi.org/10.1007/s10592-015-0734-0

Moore, I. T., Greene, M. J., Lerner, D. T., Asher, C. E., Krohmer, R. W., Hess, D. L., Whittierg, J., & Mason, R. T. (2005). Physiological evidence for reproductive suppression in the introduced population of brown tree snakes (*Boiga irregularis*) on Guam. *Biological Conservation*, **121**(1), 91–98. https://doi.org/10.1016/j.biocon.2004.04.012

Ogle, D. H. (2018). *Introductory fisheries analyses with R*. Chapman and Hall/CRC. https://doi.org/10.1201/9781315371986

Ogle, D. H., Doll, J. C., Wheeler, A. P., & Dinno, A. (2023). *FSA: Simple Fisheries Stock Assessment Methods*. R package version 0.9.4. https://CRAN.R-project.org/package=FSA

Park, K. (2004). Assessment and management of invasive alien predators. *Ecology and Society*, **9**(2), 12.

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, **118**(12), 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Picó, G., Fernández, M. J., Moreno, J. E., & Colomar, V. (2019). *Control of the ladder snake (Rhinechis scalaris) on Formentera using experimental live-traps*. Island invasives: Scaling up to meet the challenge, 1, 332–336.

Pinya, S., & Carretero, M. A. (2011). The Balearic herpetofauna: A species update and a review on the evidence. *Acta Herpetologica*, **6**(1), 59–80. https://doi.org/10.1400/179170

Piquet, J. C., & López-Darias, M. (2021). Invasive snake causes massive reduction of all endemic herpetofauna on gran Canaria. *Proceedings of the Royal Society. B, Biological sciences*, **288**(1964), 20211939. https://doi.org/10.1098/rspb.2021.1939

Pleguezuelos, J. M. (2019). Culebra de escalera - *Zamenis scalaris*. In P. López, J. Martín, & F. Martínez-Freiría (Eds.), *Enciclopedia virtual de los vertebrados Españoles* (pp. 18–20). Museo Nacional de Ciencias Naturales.

Pleguezuelos, J. M., & Brito, J. C. (2008). *Elaphe scalaris* (Schinz, 1822), Cobra-de-escada. In A. Loureiro, N. Ferrand de Almeida, M. A. Carretero, & O. S. Paulo (Eds.), *Atlas dos Anfíbios e Répteis de Portugal* (pp. 172–173). Instituto da Conservaçao da Natureza e da Biodiversidade.

Pleguezuelos, J. M., & Feriche, M. (2006). Reproductive ecology of a Mediterranean ratsnake, the ladder snake *Rhinechis scalaris* (Schinz, 1822). *The Herpetological Journal*, **16**(2), 177–182.

Pleguezuelos, J. M., Fernández-Cardenete, J. R., Honrubia, S., Feriche, M., & Villafranca, C. (2007). Correlates between morphology, diet and foraging mode in the ladder Snake *Rhinechis scalaris* (Schinz, 1822). *Contributions to Zoology*, **76**(3), 179–186.

Pleguezuelos, J. M., & Honrubia, S. (2002). *Elaphe scalaris* (Schinz, 1822). In J. M. Pleguezuelos, R. Márquez, & M. Lizana (Eds.), *Atlas y Libro Rojo de los Anfibios y Reptiles de España* (pp. 274–276). Organismo Autónomo Parques Nacionales.

Plummer, M. V. (1985). Demography of green snakes (*Opheodrys aestivus*). *Herpetologica*, **41**(4), 373–381.

Pollock, J. F. (2006). Detecting population declines over large areas with presence-absence, time-to-encounter, and count survey methods. *Conservation Biology*, **20**(3), 882–892. https://doi.org/10.1111/j.1523-1739.2006.00342.x

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.R-project.org/

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, **191**, 1–382.

Riedle, J. D. (2014). Demography of an urban population of ring-necked snakes (*Diadophis punctatus*) in Missouri. *Herpetological Conservation and Biology*, **9**(2), 278–284.

Rodda, G. H., & Fritts, T. H. (1992). The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam's lizards. *Journal of Herpetology*, **26**(2), 166–174.

Rodda, G. H., Fritts, T. H., & Chiszar, D. (1997). The disappearance of Guam's wildlife. *Bioscience*, **47**(9), 565–574. https://doi.org/10.2307/1313163

Rodda, G. H., & Savidge, J. A. (2007). Biology and impacts of Pacific Island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae). *Pacific Science*, **61**(3), 307–324. https://doi.org/10.2984/1534-6188(2007)61[307:BAIOPI]2.0.CO;2

Rodríguez de Rivera, O., & McCrea, R. (2021). Removal modelling in ecology: A systematic review. *PLoS One*, **16**(3), e0229965. https://doi.org/10.1371/journal.pone.0229965

Rose, J. P., Miano, O. J., & Todd, B. D. (2013). Trapping efficiency, demography, and density of an introduced population of northern Watersnakes, *Nerodia sipedon*, in California. *Journal of Herpetology*, **47**(3), 421–427. https://doi.org/10.1670/12-119

Roy, H. E., Lawson Handley, L. J., Schönrogge, K., Poland, R. L., & Purse, B. V. (2011). Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? *BioControl*, **56**(4), 451–468. https://doi.org/10.1007/s10526-011-9349-7

Sardá, F. (1998). Symptoms of overexploitation in the stock of the Norway lobster (*Nephrops norvegicus*) on the "Serola Bank" (Western Mediterranean Sea off Barcelona). *Scientia*

*Marina*, **62**(3), 295–299. https://doi.org/10.3989/scimar.1998.62n3295
Savidge, J. A. (1991). Population characteristics of the introduced brown tree snake (*Bioga irregularis*) on Guam. *Biotropica*, **23**(3), 294–300.
Schamber, J. L., Esler, D., & Flint, P. L. (2009). Evaluating the validity of using unverified indices of body condition. *Journal of Avian Biology*, **40**(1), 49–56. https://doi.org/10.1111/j.1600-048X.2008.04462.x
Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of mass–size residuals: Validating body condition indices. *Ecology*, **86**(1), 155–163. https://doi.org/10.1890/04-0232
Shine, R., Branch, W. R., Webb, J. K., Harlow, P. S., Shine, T., & Keogh, J. S. (2007). Ecology of cobras from southern Africa. *Journal of Zoology*, **272**(2), 183–193. https://doi.org/10.1111/j.1469-7998.2006.00252.x
Shwiff, S. A., Gebhardt, K., Kirkpatrick, K. N., & Shwiff, S. S. (2010). Potential economic damage from introduction of Brown tree snakes, *Boiga irregularis* (Reptilia: Colubridae), to the islands of Hawai'i. *Pacific Science*, **64**(1), 1–10. https://doi.org/10.2984/64.1.001
Silva-Rocha, I., Salvi, D., Sillero, N., Mateo, J. A., & Carretero, M. A. (2015). Snakes on the Balearic Islands: An invasion tale with implications for native biodiversity conservation. *PLoS One*, **10**(4), e0121026. https://doi.org/10.1371/journal.pone.0121026
Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pysek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, **28**, 58–66. https://doi.org/10.1016/j.tree.2012.07.013
Soto, I., Cuthbert, R. N., Kouba, A., Capinha, C., Turbelin, A., Hudgins, E. J., Diagne, C., Courchamp, F., & Haubrock, P. J. (2022). Global economic costs of herpetofauna invasions. *Scientific Reports*, **12**(1), 10829. https://doi.org/10.1038/s41598-022-15079-9
Steen, D. A. (2010). Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation and Biology*, **5**(2), 183–188.
Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *Bioscience*, **45**(11), 759–771. https://doi.org/10.2307/1312628
Vericad, J. R., & Escarré, A. (1976). Datos de alimentación de ofidios en el Levante sur ibérico. *Mediterránea*, **1**, 5–33. https://doi.org/10.14198/MDTRRA1976.1.01
Vigne, J. D., & Alcover, J. A. (1985). *Incidence des rélations historiques entre l'homme et l'animal dans la composition actuelle du peuplement amphibien, reptilien et mammalien des îles de Mediterranée occidentale*. Actes du 110ème Congrés National des Sociétés Savantes (pp. 79–91).
Ward, R. J., Griffiths, R. A., Wilkinson, J. W., & Cornish, N. (2017). Optimising monitoring efforts for secretive snakes: A comparison of occupancy and N-mixture models for assessment of population status. *Scientific Reports*, **7**(1), 1–12. https://doi.org/10.1038/s41598-017-18343-5
Weatherhead, P. J., & Brown, G. P. (1996). Measurement versus estimation of condition in snakes. *Canadian Journal of Zoology*, **74**(9), 1617–1621. https://doi.org/10.1139/z96-179
Whittier, J. M., & Limpus, D. (1996). Reproductive patterns of a biologically invasive species: The brown tree snake (*Boiga irregularis*) in eastern Australia. *Journal of Zoology*, **238**(3), 591–597. https://doi.org/10.1111/j.1469-7998.1996.tb05416.x
Wiles, G. J., Bart, J., Beck, R. E., Jr., & Aguon, C. F. (2003). Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology*, **17**(5), 1350–1360. https://doi.org/10.1046/j.1523-1739.2003.01526.x
Willson, J. D., Dorcas, M. E., & Snow, R. W. (2011). Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in southern Florida. *Biological Invasions*, **13**(7), 1493–1504. https://doi.org/10.1007/s10530-010-9908-3
Winne, C. T., Willson, J. D., & Whitfield Gibbons, J. (2010). Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake, *Seminatrix pygaea*. *Oecologia*, **162**(4), 913–922. https://doi.org/10.1007/s00442-009-1513-8
Zhang, L., Rohr, J., Cui, R., Xin, Y., Han, L., Yang, X., Gu, S., Du, Y., Liang, J., Wang, X., Wu, Z., Hao, Q., & Liu, X. (2022). Biological invasions facilitate zoonotic disease emergences. *Nature Communications*, **13**(1), 1–11. https://doi.org/10.1038/s41467-022-29378-2
Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

**Legislation**

Decret llei 1/2023. (2023). *de 30 de gener, de mesures extraordinàries i urgents per a la protecció de la sargantana pitiüsa (Podarcis pityusensis) i la sargantana balear (Podarcis lilfordi) i per a la prevenció i lluita contra les espècies de la família Colubridae sensu lato. BOIB núm. 15, de 2 de febrer de 2023.*
Real Decreto 630/2013. (2013). *de 2 de agosto, por el que se regula el Catálogo español de especies exóticas invasoras. «BOE» núm. 185, de 3 de agosto de 2013. Reference: BOE-A-2013-8565.*

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Data S1.** Script used to generate the statistical analyzes carried out in the present work.

**Table S1.** Mean ± standard deviation (SD), range (minimum value–maximum value) and sample size of fat percentage (%)

and snout-vent length (SVL, cm) of males, females and total of the population sampled during the years 2017–2020. Data about fat percentage were not available for the year 2017.

**Table S2.** Mean fat percentage (%) of adult females obtained during the sampling months of the years 2018 ($n$ = 79), 2019 ($n$ = 20) and 2020 ($n$ = 48).

**Fig. S1.** Trap baited with a live mouse designed by the Department of Health and Control of Fauna of the COFIB and used for capturing the snakes analyzed in the present work.

**Fig. S2.** Leslie depletion curve depicting the regression between weekly catch per unit effort (CPUE, which is mentioned as CPE in the package 'FSA') and cumulative catch of *Zamenis scalaris* in (a) 2017, (b) 2018, (c) 2019 and (d) 2020 in Formentera. Also, $R^2$ and P are also shown in each case.